The Wilson Journal of Ornithology 118(1):59–63, 2006

FIELD EXPERIMENTS ON EGGSHELL REMOVAL BY MOUNTAIN PLOVERS

TEX A. SORDAHL[1]

ABSTRACT.—I conducted 18 eggshell removal trials at six Mountain Plover (*Charadrius montanus*) nests in the Pawnee National Grassland, Weld County, Colorado, during June 1994. Eggshell fragments were placed at various distances (10 cm to 10 m) from active nests. Attending adult plovers removed eggshells throughout the incubation period. When eggshells were placed within 2 m of the nest, plovers usually removed them immediately upon their return to the nest. Shells placed farther away—up to 10 m—were removed after longer time intervals. Plovers removed shells by picking them up with their bills and running or flying away with them before dropping them 6 to 100 m from the nest. When returning to their nests, plovers approached by ground. Of the five hypotheses proposed in the literature to explain the function of eggshell removal behavior in birds, only one (reducing cues predators might use for finding nests) predicts removal of shells already outside the nest and disposal of shells far from the nest. Thus, my results support an anti-predator function for eggshell removal in Mountain Plovers. *Received 3 November 2004, accepted 1 October 2005.*

Shortly after their young hatch, many birds remove the empty eggshells and dispose of them away from the nest (Nethersole-Thompson and Nethersole-Thompson 1942, Skutch 1976). This behavior is well developed in charadriiform birds, including shorebirds and gulls. In their classic paper, Tinbergen et al. (1962) suggested five possible hypotheses for the adaptive value of eggshell removal behavior: (1) eggshells might provide cues that would attract predators to the nest; (2) later-hatching eggs might become encapsulated, the young in hatching eggs thus becoming trapped inside a double shell (termed "egg-capping" by Derrickson and Warkentin 1991); (3) sharp edges of shells might injure chicks in the nest; (4) organic material associated with eggshells might promote growth of pathogenic bacteria and mold in the nest; and (5) hatched shells could interfere with brooding chicks in the nest. Tinbergen's field experiments with gull eggs, which are cryptically colored externally but conspicuously white inside, supported the first hypothesis by showing that artificial nests with eggshells nearby experienced greater predation rates than those without nearby eggshells (Tinbergen et al. 1962, Tinbergen 1963). Tinbergen, however, did not rule out the remaining hypotheses. Subsequent literature has tended to support the predation (Sordahl 1994, Sandercock 1996) and egg-capping hypotheses (Derrickson and Warkentin 1991, Sandercock 1996, Verbeek 1996, Hauber 2003).

Hypotheses 3, 4, and 5 seem unlikely explanations of the evolution of eggshell removal behavior in shorebirds because their eggs usually hatch synchronously and the precocial young leave the nest within 24 hr of hatching. Sandercock (1996) reported observations of egg-capping in two sandpiper species, supporting hypothesis 2. However, he recognized that egg-capping alone could not account for the form of removal behavior typically seen in shorebirds—specifically, the disposal of eggshells far from the nest—and concluded that both egg-capping and predation have contributed to the evolution of eggshell removal behavior in these birds.

Here, I report the results of field trials on eggshell removal behavior of Mountain Plovers (*Charadrius montanus*). Mountain Plovers nest on the ground in very open habitat, where predation is the major cause of egg and chick losses (Graul 1975, McCaffery et al. 1984, Sordahl 1991, Miller and Knopf 1993, Knopf 1996, Knopf and Rupert 1996). General aspects of eggshell removal in this species were described by Graul (1975). My experiments enabled me to provide a quantitative description of the behavior and to evaluate its function.

METHODS

I performed field trials on eggshell removal by Mountain Plovers from 9 to 18 June 1994 at Pawnee National Grassland, Weld County,

[1] Dept. of Biology, Luther College, Decorah, IA 52101, USA; e-mail: sordahlt@luther.edu

TABLE 1. Results of 18 field trials on eggshell removal behavior at six Mountain Plover nests, Pawnee National Grassland, Colorado, 9–18 June 1994. In each trial, one-third of a complete eggshell (of Mountain Plover or Japanese Quail) was placed near the nest and the behavior of the adult was observed upon its return to the nest.

Nest[a]	Incubation day	Shell type	Nest–shell distance (m)	Time until removal (min)	Removal method	Disposal distance (m)
S1	5	Quail	0.5	0.08	Fly	70
S1	6	Quail	0.7	10	—[b]	—
S1	7	Quail	0.6	0	Fly	60
K1	7	Quail	1.0	0	Run-fly	30
K1	8	Quail	0.5	0.17	Run	6
K1	8	Quail	2.5	97	Run	17
K1	8	Quail	5.0	105	—	—
K1	8	Quail	10.0	—	—	22
K1	9	Quail	1.5	26	—	—
S2[c]	8	Quail	0.2	0	Run	20
S2	8	Quail	0.5	0	Run	30
K2	15	Plover	2.0	3	Run-fly	100
K2	16	Quail	3.0	0	Run	18
K2	16	Quail	4.0	69	—	—
R1	20	Plover	0.1	0	Run	12
R1	23	Plover	0.3	0	Fly	90
R1	25	Quail	0.7	0	Run	15
K3	27	Plover	1.5	0	Run	18

[a] Mountain Plovers typically exhibit uniparental care; therefore, egg removals were assumed to represent the behavior of one adult per nest.
[b] Missing data in the table indicate that shell removal was not observed (see text) or that the disposed shell was not found.
[c] Nest S2 contained four eggs; all other nests contained three.

Colorado (40° 45′ N, 104° 00′ W). This shortgrass prairie site has been well described elsewhere (Graul 1973, 1975; McCaffery et al. 1984). Its vegetation was very short and sparse, and it was grazed by cattle.

I studied eggshell removal at six Mountain Plover nests. Five nests contained three-egg clutches (normal for Mountain Plovers) and one nest contained four eggs. The attending adults were not marked for identification, but since uniparental care is typical in this species (Knopf 1996), it is likely that I tested six different individuals. Mountain Plovers are sexually monomorphic (Hayman et al. 1986, Knopf 1996), so I was unable to determine the sex of the birds. Trials entailed placing approximately one-third of a complete eggshell on the ground (interior—or white—side up) at various distances (ranging from 10 cm to 10 m) from the nest and then observing the behavior of the adult when it returned to its nest. I conducted 18 trials, 14 with Japanese Quail (*Coturnix japonica*) eggshells obtained commercially and 4 with Mountain Plover eggshells that I found opportunistically in the field. The two species' shells are similar in size and appearance, both having earth-tone background colors and dark, irregular markings. Adult plovers responded similarly to the two kinds of shells; therefore, I pooled the results.

Observations were made from a vehicle about 100 m from nests with 7 × 35 binoculars. For each trial, I recorded the nest-to-shell distance, the amount of time elapsed between the adult's return to the nest and removal of the shell, the removal method (run or fly), the disposal distance, and the method (run or fly) of returning to the nest after shell disposal. At least one egg hatched in every nest and, assuming that incubation begins when the clutch is complete and the average incubation period is 29 days (Knopf 1996), I used backdating to determine days since incubation began. I measured the distances of eggshells from nests with a tape measure, and disposal distances of shells that I was able to relocate by pacing.

RESULTS

The number of trials conducted at each of the six nests was 6, 3, 3, 3, 2, and 1 (Table 1). The attending adult Mountain Plover removed shells at all six nests. Nine of 18 shells

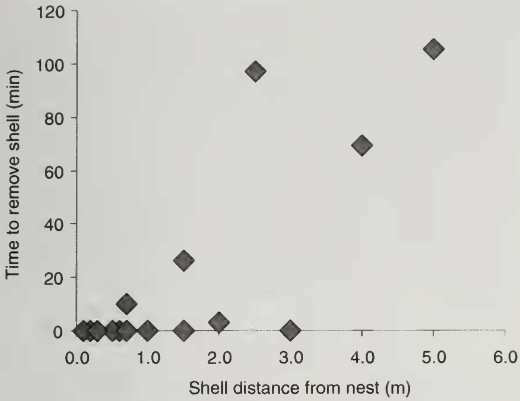

FIG. 1. Relationship between the distance eggshells were placed from Mountain Plover nests and the time elapsed before the adult removed the shell, 9–18 June 1994, Pawnee National Grassland, Weld County, Colorado. Three of the 17 points overlap at 0.5 m (2 are hidden).

were removed immediately upon the adult's return to the nest; 2 more were removed within 10 sec. Two other shells were removed 3 min and 10 min after the adults had returned. Four of the remaining five shells were removed in less than 2 hr. The final shell, placed 10 m from the nest, was not removed during 15 min of observation, at which time I departed the nest site; the following morning I found the shell 22 m from the nest. Although it is possible that the wind or another animal moved this shell, it seems most likely that the adult plover moved it. Overall, shells placed within 2 m of the nest were removed promptly (most of them immediately), whereas shells placed farther away were removed after longer intervals (Fig. 1). Eggshell removal was documented on incubation days 5–9, 15, 16, 20, 23, 25, and 27 (Table 1).

I recorded eggshell removal and adult return to the nest for 13 of 18 trials (Table 1). During the remaining five trials, which had long eggshell removal times, my vigilance was intermittent and I did not observe the actual removal. However, by checking for the eggshell as soon as I noticed that the bird was off the nest, I was able to record removal times with only a small margin of error (except in the case described above, where I left the site before removal occurred). When a Mountain Plover removed an eggshell, it picked the shell up with its bill and ran away with it (8 of 13 observations), flew off with it (3 of 13 observations), or ran 2–3 m before flying off with it (2 of 13 observations). On 14 occasions I was able to recover shells where they were dropped; disposal distances ranged from 6 to 100 m from the nest (Table 1). Plovers tended to dispose of shells at greater distances when they flew (mean = 70.0 m, range = 30–100, n = 5) than when they ran (mean = 17.0 m, range = 6–30, n = 8). On four occasions I recorded which facet (inside or outside) of a recovered shell was exposed; two shells were lying with the cryptic outside facing up and two were lying with the conspicuous inside of the shell facing upward. After disposing of the shells, adults always returned to their nests by a ground approach (13 of 13 observations), which is typical of plovers (TAS pers. obs.).

DISCUSSION

My field experiments demonstrated that Mountain Plovers remove eggshells throughout the incubation period. This may be true for most birds, and the expression of the behavior long before hatching occurs likely has been selected for in the context of removal of damaged eggs (Nethersole-Thompson and Nethersole-Thompson 1942, Montevecchi 1976, Kemal and Rothstein 1988, Sordahl 1994). Removal of dead chicks from the nest also has been reported (Nethersole-Thompson 1951:183, Skutch 1976:284, Sordahl 1994).

Because it had already been demonstrated that Mountain Plovers remove eggshells located *in* their nests (Graul 1975, Knopf 1996; TAS pers. obs.), I designed my experiments to determine whether they would remove shells placed outside the nest and, if so, how far from the nest they would go to remove shells. I observed adults immediately remove shells that had been placed up to 3 m from their nests (Table 1, Fig. 1). They also eventually removed shells at distances of 4, 5, and probably 10 m, as well. Because the average disposal distance was only 17 m for birds that removed eggshells by running, it seems unlikely that Mountain Plovers would remove shells located much farther from their nests than 10 m.

The closer a shell was placed to the nest, the more quickly it was removed (Fig. 1). The proximate explanation for this probably is that adults were less likely to detect eggshells that were farther from the nest. Even though Mountain Plover nesting habitat is shortgrass prairie, the line of sight a plover has when making a ground approach to its nest is low enough that even small obstructions could interfere with its ability to notice a distant shell. An ultimate explanation for this finding would be that the risk of predation due to the presence of eggshells diminishes with distance from the nest, as shown by Tinbergen et al. (1962) for Black-headed Gull (*Larus ridibundus*) eggs. Tinbergen et al. (1962) found that a broken eggshell ≤1 m from an artificial clutch increased the predation rate, but an eggshell 2 m away did not. If the radius of increased risk is similar for Mountain Plovers, one might expect them to be less diligent about removing shells >2 m from the nest. My results are consistent with this because the birds did not immediately remove shells that were >2–3 m away. Nevertheless, they eventually did remove those shells, which suggests that such shells pose at least some risk to the clutch.

Although eggshell removal and disposal distances have not been investigated systematically in birds, these distances most likely represent a compromise between the benefits of removal and the costs of leaving the nest when young are hatching. Factors that probably influence these distances are habitat (especially open habitats in the case of Mountain Plovers), the degree of nest dispersion (widely spaced in Mountain Plovers), and which species of egg and chick predators inhabit the area (mammals and snakes are thought to be important predators of Mountain Plovers; Knopf 1996).

Of the five hypotheses explaining the adaptive value of eggshell removal, the only one that predicts removal of eggshells already outside the nest is the predation hypothesis. It also is the only hypothesis that predicts disposal far from the nest. Thus my results support an anti-predator function for eggshell removal in Mountain Plovers. Similarly, fecal sac removal by many nidicolous birds (which is analogous to eggshell removal) involves disposal of fecal sacs far from the nest (Petit et al. 1989 and references therein), and this behavior also seems best explained as a means of reducing cues that could lead predators to nests (Petit et al. 1989, Lang et al. 2002). However, I cannot rule out the possibility that eggshell removal serves functions other than predation avoidance. For example, if there is a risk that wind may blow shells back into the nest, it may be adaptive to dispose of them far away so they do not threaten the chicks with encapsulation or injury. Further research is needed to examine these alternative explanations of eggshell removal behavior.

ACKNOWLEDGMENTS

I especially thank C. A. Ristau for enabling me to study Mountain Plovers in Colorado. She and F. L. Knopf generously shared information about nests they had found. The manuscript benefited from comments by D. I. Bishop, S. J. Dinsmore, M. B. Wunder, and two anonymous referees. This research was conducted, in part, on the Central Plains Experimental Range operated by the USDA Agricultural Research Service and made available to the Long Term Ecological Research Program administered by Colorado State University. I thank M. Lindquist for courtesies extended during my stay. I was supported by a Luther College Faculty Research Grant.

LITERATURE CITED

Derrickson, K. C. and I. G. Warkentin. 1991. The role of egg-capping in the evolution of eggshell removal. Condor 93:757–759.

Graul, W. D. 1973. Adaptive aspects of the Mountain Plover social system. Living Bird 12:69–94.

Graul, W. D. 1975. Breeding biology of the Mountain Plover. Wilson Bulletin 87:6–31.

Hauber, M. E. 2003. Egg-capping is a cost paid by hosts of interspecific brood parasites. Auk 120: 860–865.

Hayman, P., J. Marchant, and T. Prater. 1986. Shorebirds: an identification guide to the waders of the world. Houghton Mifflin, Boston, Massachusetts.

Kemal, R. E. and S. I. Rothstein. 1988. Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. Animal Behaviour 36: 175–183.

Knopf, F. L. 1996. Mountain Plover (*Charadrius montanus*). The Birds of North America, no. 211.

Knopf, F. L. and J. R. Rupert. 1996. Reproduction and movements of Mountain Plovers breeding in Colorado. Wilson Bulletin 108:28–35.

Lang, J. D., C. A. Straight, and P. A. Gowaty. 2002. Observations of fecal sac disposal by Eastern Bluebirds. Condor 104:205–207.

McCaffery, B. J., T. A. Sordahl, and P. Zahler. 1984. Behavioral ecology of the Mountain Plover in northeastern Colorado. Wader Study Group Bulletin 40:18–21.

Miller, B. J. and F. L. Knopf. 1993. Growth and survival of Mountain Plovers. Journal of Field Ornithology 64:500–506.

Montevecchi, W. A. 1976. Eggshell removal by Laughing Gulls. Bird-Banding 47:129–135.

Nethersole-Thompson, C. and D. Nethersole-Thompson. 1942. Egg-shell disposal by birds. British Birds 35:162–169, 190–200, 214–223, 241–250.

Nethersole-Thompson, D. 1951. The Greenshank. Collins, London, Great Britain.

Petit, K. E., L. J. Petit, and D. R. Petit. 1989. Fecal sac removal: do the pattern and distance of dispersal affect the chance of nest predation? Condor 91:479–482.

Sandercock, B. K. 1996. Egg-capping and eggshell removal by Western and Semipalmated sandpipers. Condor 98:431–433.

Skutch, A. F. 1976. Parent birds and their young. University of Texas Press, Austin.

Sordahl, T. A. 1991. Antipredator behavior of Mountain Plover chicks. Prairie Naturalist 23:109–115.

Sordahl, T. A. 1994. Eggshell removal behavior of American Avocets and Black-necked Stilts. Journal of Field Ornithology 65:461–465.

Tinbergen, N. 1963. The shell menace. Natural History 72(7):28–35.

Tinbergen, N., G. J. Broekhuysen, F. Feekes, J. C. W. Houghton, H. Kruuk, and E. Szulc. 1962. Egg shell removal by the Black-headed Gull, *Larus ridibundus* L.: a behaviour component of camouflage. Behaviour 19:74–117.

Verbeek, N. A. M. 1996. Occurrence of egg-capping in birds' nests. Auk 113:703–705.